POLLINATION ECOLOGY OF *EUPHORBIA GENICULATA* (EUPHORBIACEAE)[1]

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(With a plate & three text-figures)

Euphorbia geniculata is monoecious and reproduces both by geitonogamy and xenogamy. The stigmas are fully receptive by the 3rd day of anthesis, and the male phase is evident from the 5th day of female anthesis, with the anthers dehiscing between 0800-1000 h. The nectar is glucose + fructose dominant type, and is secreted in quantity by day and night. The cyathium is flat blossom and is of the promiscous type. Pollination is effected by a broad spectrum of diurnal insects and is of the 'mess and soil' type. The principal pollinators are ants (*Camponotus*), wasps (*Ropalidia, Polistes, Vespa*) and beetles (*Coccinella*). The ants are consistent and more abundant, and they alone could satisfy the pollination requirement to result in 100% reproductive success. The ants because of their crawling behaviour mainly deliver geitonogamous pollen, but their bellicose nature helps the plant to achieve more outcrossing by the wasps which being scared of the ants move more often from plant to plant.

Introduction

In the family Euphorbiaceæ, the genus *Euphorbia* is the largest one represented by more than 1600 species (Lawrence 1973), all of which are almost cosmopolitan in distribution, but majority confined to the tropics (Kerner 1904, Good 1964). The cyathial morphology and anatomy were fully studied by several generations of botanists since Roeper's day and the basic structure is now well understood; however, this knowledge has never been related effectively to pollination problems (Webster 1967).

The early works reported diverse groups of insects visiting 18 species of *Euphorbia* (Knuth 1906-9); however the importance of insects in the reproductive biology of these plants remained obscure. Only very recently has there been a detailed study by Ehrenfeld (1976, 1979) in respect of three species of *Euphorbia,* sub-genus *Chamaesyce.* His results showed that the three species differ in their reliance on insect vectors for reproduction. Despite such scattered observations, the floral biology of the genus *Euphorbia* characterised by unique floral device is still rather poorly known (Webster 1967, Ehrenfeld 1976). Realising the importance and dearth of these studies from the tropical zones, especially of the Indian subcontinent, attempts were made to collect the data on pollination ecology of *Euphorbia geniculata,* a monoecious annual weed occurring in the cultivated fields and gardens, and growing to 1 m height.

Materials and Methods

Euphorbia geniculata Orteg. (*E. heterophylla* L.) growing at Visakhapatnam in the cultivable lands of the Botany Experimental

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Farm area 3 km away from the Andhra University Campus on NH5 formed the material for the present study. Fifty cyathia labelled in bud condition were followed till they ceased to produce flowers to record daily anthesis from which the male to female flower ratio was computed. Numerical assessment of the pollen grains contained in an anther was made squashing the mature and undehisced anther in lactophenol aniline-blue and counting the entire pollen mass drawn into a band on the microscope slide. Periodic determinations of the pollen contained in the dehisced anthers were similarly done. The pollen grains deposited on the stigmas were counted after pressing the stigmas in between two glass slides. The longevity of pollen was assessed through *in vitro* germination studies using 20% sucrose solution with 1% boric acid solution added. The length of the stigma receptivity was based on pollen germination after hand pollinating the stigmas of different ages.

To monitor the nectar amounts, the plants in bloom were covered with insect proof cages for the required periods and DDT was applied around the plants to prevent the ants reaching the nectar cups. The nectar accumulated in the cups was measured at intervals using dispensable micropipettes. Sugar concentration was read with Erma Hand Refractometer and sugar composition using paper chromatography and spectrophotometry (Harborne 1973). Proteins and amino acids were detected according to Baker & Baker (1973).

The insects caught at the cyathia all through the study period (1979 and 1980) were got identified through the courtesy of CIE London. Green house was used to study the prevailing breeding system(s) and to estimate the reliance on insects for pollination. Sticky cylinders were exposed daily for a week at the plants' height to assess the role of wind in pollen dispersal. To assess the efficacy of ants *versus* other foragers as pollinators, certain plants were allowed to receive the foragers excluding the ants through applying DDT at the plant bases. Another batch of plants were open to ant visits only. After leaving sufficient time, the fruits and the seeds formed, were scored and compared.

The number of cyathia visited in a bout and per unit time, and the time spent on a cyathium by each major insect species were recorded using a stop watch. The more frequent visitors were caught at the cyathia and were washed with alcohol. After adding a droplet of lactophenol aniline-blue, these washings were observed for pollen under light microscope. To determine the number of pollen that could be transferred on to the stigmas by a single visit of a particular kind of insect visitor, plants in bloom kept in insect-free cages were opened in batches for the insects to visit; when such exposed cyathia received the first visit they were plucked and their stigmas examined for pollen. Several such observations were done and the mean number of pollen transferred, was calculated.

Observations

Floral dynamics

The plants are evident in any part of the year provided the soil contains enough moisture. Normally, these appear after the first rains. After a month's vegetative growth, the plants bloom, the blooming normally lasting for $1\frac{1}{2}$ to 2 months.

Inflorescence. It is a cyathium. Several such cyathia (45 ± 18) are arranged in terminal condensed dichasia of 3.5-4.0 cm in diameter. Cyathium is glabrous without and consists of an ovoid involucre with the margin lined with a fringe of fleshy, finger-like lobes. A con-

TABLE 1

RATE OF ANTHER DEHISCENCE IN *E. geniculata* ON FOUR DIFFERENT OCCASIONS IN RELATION TO THE PREVAILING WEATHER

Time (h)	8-5-1979			11-5-1979			12-5-1979			16-5-1979		
	i	ii	iii	i	ii	iii	i	ii	iii	i	ii	iii
0600	27.0	85	0	27.0	90	0	27.0	90	0	27.0	81	0
0700	28.0	83	0	27.0	90	0	27.0	90	0	27.3	80	0
0800	28.5	80	0	26.5	95	0	27.7	88	0	27.5	79	75
0900	33.2	70	75	28.2	90	0	27.5	88	0	28.5	75	25
1000	34.0	65	25	28.5	90	0	28.0	85	0			
1100				31.1	70	21	28.0	85	0			
1200				31.8	68	4	28.0	83	0			
1300				30.0	80	6	28.0	80	0			
1400				29.5	77	0	28.0	82	0			
1500				27.0	80	0	28.0	85	0			
1600				27.0	80	0	28.2	83	0			
1700				27.0	80	0	28.2	84	0			
1800				27.0	80	0	28.2	83	0			
	Partly cloudy sky			Rain intermittent			Rain continuous			Clear sky		

i = Temperature (°C); ii = Relative humidity (%), iii = No. of dehisced anthers Sample size = 100 male flowers.

spicuous, fleshy, terete, stipitate gland with slightly flared round opening is situated on the involucre to a side. In rare cases 2-4 such glands are noticed.

Each cyathium is normally bisexual, but occasionally the female part is suppressed. Out of the 550 cyathia examined, 85% bore both female and male flowers, whereas 15% consisted of only male flowers.

Staminate flowers. Several male flowers surrounding the female are located within the involucre. They also lack perianth and each one is monandrous with the subglobose, 2-lobed anthers being borne on a pedicel of 3 mm long. The male phase of the cyathium is evident from the 5th day of female anthesis. The anther starts getting exserted above the rim of the cyathium from 0600 h and is fully exserted by 0800 h. Anther dehiscence is accomplished by the horizontal fissure on the side of the anther facing upwards, when the

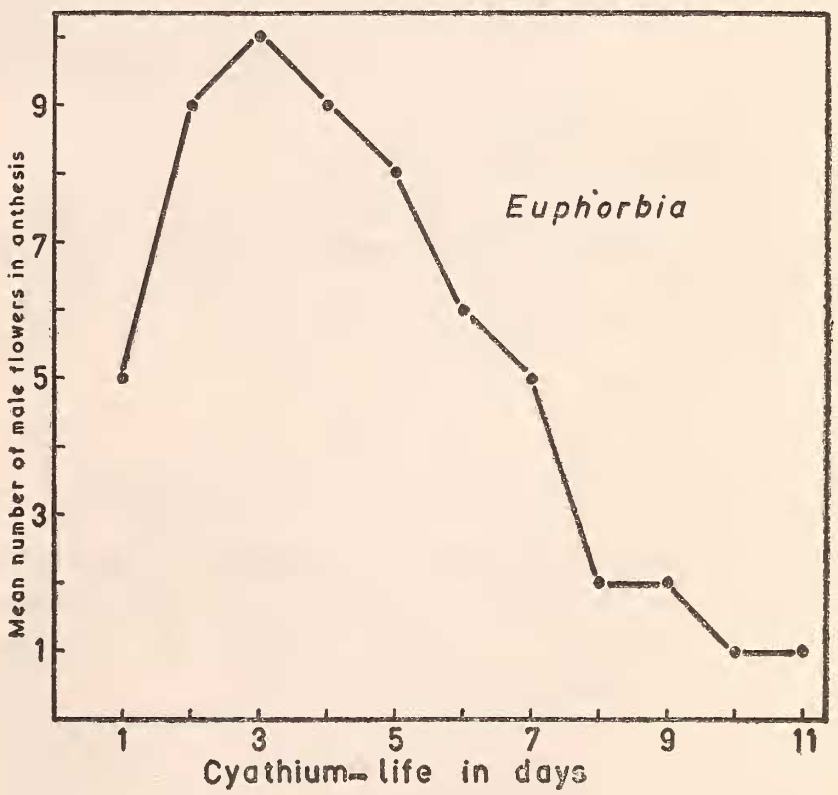

Fig. 1. Day to day anthesis of male flowers in the life-time of the cyathium of *Euphorbia geniculata.*

ambient temperature approaches 28-32°C and RH 70-75% (Table 1). If the conditions are wet as on a rainy day, the process is suppressed and the anthers being ephemeral drop away the next morning.

Each day varying numbers of male flowers attain maturity (Fig. 1) and over the entire period (8±2, R.6-11 days) of male phase, 55±11 (R. 39-68) flowers emerge out.

Pollen morphology. The pollen grains are subspheroidal, tricolporate, 56±5 μm (R. 48-64) with the modal class of 56 μm, and the exine is reticulate.

Pollen supply. The number of grains per male flower varied between 276-445, the average being 370±42 (n=20).

Pollen viability. About 12% of the pollen per male flower are sterile as evidenced by their abnormal size, shape and poor stainability with lactophenol aniline-blue.

Germ tube initiation occurred after 15 min. of placing the grains in the medium; the tubes burst after 3 hrs. On an average 88% of the freshly collected pollen germinated. The same sample of pollen showed 80% germination after 24 hours of storage in the laboratory. The germination per cent fell drastically after 48 hours, and after 72 hours there is none.

Pistillate flowers. Each cyathium bears a solitary and centrally located female flower lacking perianth. A 3-celled ovary with a single ovule in each cell, is supported on a rather prominent stalk. Styles are 3, connate at the base; each stigma is bifid.

Maturation of the female flower. Figure 2 represents the different stages in the maturation of the female flower. The exsertion of the stylar column above the rim of the cyathium

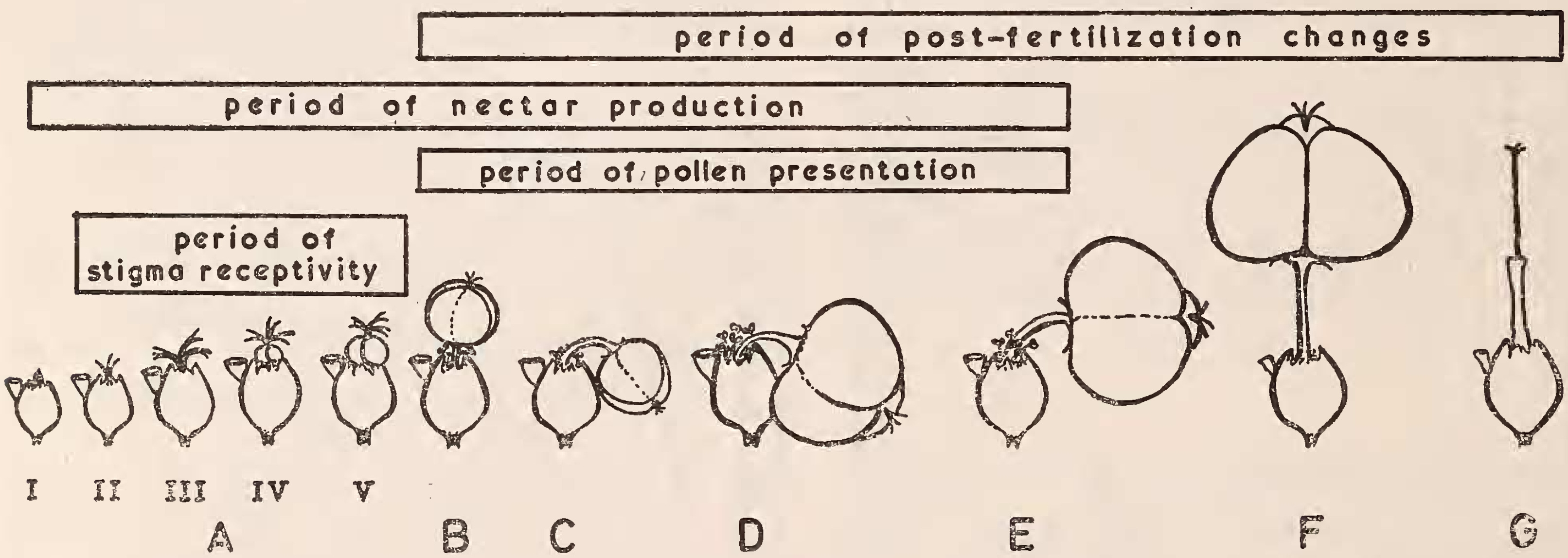

Fig. 2. Pictorial representation of the different reproductive phases in a cyathium of *Euphorbia geniculata*: A — Female phase with the stigma in various maturation stages (I — stigma exserting, II — stigma tripartite and shiny, III — stigma well developed, reflexed and shiny, IV — ovary partly exserted and the stigma shiny, V — ovary fully exserted and the stigma shiny); B — Male phase commenced and the ovary (fruit) stalk started reflexing; C & D — Ovary stalk fully reflexed and the anthers are freely exposed; E — Male phase ceased and the ovary stalk is in the process of resuming its original erect posture; F — Ovary stalk has regained its original erect posture and the nectar cup is in the shrunken state; G — the stalk after the dehiscence of the fruit.

marks the beginning of anthesis. It occurs in the morning after sunrise, but may vary with the age of the flower. By this time traces of nectar are detectable in the nectar cup, though it continues enlarging. By next morning the stylar column becomes tripartite and the branches start diverging and the stigmas become bifid and begin reflexing. They are slightly sticky. By the 3rd day of anthesis, the stigmas are reflexed and fully receptive. They remain in this condition for another two days. By this time the ovary is pushed out of the cyathium because of the elongation of the pedicel. The pedicel reflexes so that the ovary rests on the outside of the involucre on the side just opposite to the position of the gland; the stigmas wither and are unreceptive. The pedicel further elongates and by the 8th day of female anthesis, the ovary almost assumes an inverted position. Later it regains its original erect posture before dispersing the seeds in an explosive way.

These movements are obviously designed to give sufficient room to the anthers when they are exserted, in order that they inevitably gain contact when a proper visitor alights on the cyathium.

Pollen-Ovule ratio. On an average 7980 grains are produced to meet the demands of one ovule. Out of these only 0.223% reaches the stigma.

DYNAMICS OF NECTAR

Nectar amounts and pattern of production. Measureable amounts of nectar are produced from the 2nd day after the stigma attains receptivity and continue to be produced till the cessation of the male phase. Nectar is secreted both by day and night. On an average a cup produces 19.23 μl of nectar in its lifespan. The rate of secretion increases up to the 4th day and thence decreases till the 13th day when it ceases. The amounts secreted during the nights are comparatively more, probably because of low evaporation taking place. There is no appreciable trend in the rate of secretion, it being uniform at different times during daytime. However, the pooled up amounts exceeded the quantity removed after the entire period (Table 2).

Nectar concentration. On a normal day the

TABLE 2

NECTAR VOLUMES OF REPEAT-SAMPLED VS. ONCE-SAMPLED CUPS IN *E. geniculata* AND THE ASSOCIATED WEATHER

2 hourly samples				Sample for 12 hours
Time (h)	Temp. (°C)	RH (%)	Mean nectar volume (μl)	Mean nectar volume (μl)
0600-0800	29.4	83	0.470	
0800-1000	30.3	79	0.470	
1000-1200	32.1	68	0.460	
1200-1400	32.0	68	0.455	
1400-1600	31.8	70	0.465	
1600-1800	30.8	70	0.470	
0600-1800				2.225
Total volume			2.790	2.225
			n = 20	n = 20

TABLE 3

TEMPORAL VARIATION IN *E. geniculata* NECTAR CONCENTRATION AND THE ASSOCIATED WEATHER

Time (h)	Concentration (%)	Temperature (°C)	RH (%)
0600	25	23.8	79.0
0900	27	24.8	69.5
1200	30	26.7	67.0
1500	32	26.9	60.0
1800	29	25.0	70.0

TABLE 4

FLORAL VISITORS ON *E. geniculata*

Insect species	Forage type
HETEROPTERA	
Lygaeidae	
Geocoris ochropterus (Fieber)	Nectar
COLEOPTERA	
Coccinellidae	
Coccinella rependa (Thunberg)	Nectar & anthers
Verania discolor (F.)	Nectar & anthers
V. vincta (Gorham)	Nectar & anthers
Menochilus sexmaculatus (F.)	Nectar
Nitidulidae	
Macroura sp.	Nectar
Bruchidae	
Spermophagus sp.	Nectar
Curculionidae	
Baris dolosa (Mshl.)	Nectar
DIPTERA	
Asilidae	
Laxenecera sp.	Nectar
Bombyliidae	
Eucharimyia sp.	Nectar
Syrphidae	
Eristalinus quinquestriatus (F.)	Nectar
Otitidae	
Physiphora sp.	Nectar
Chloropidae	
Anatrichus pygmaeus (Lamb)	Nectar
Muscidae	
Musca pattoni (Austen)	Nectar
Calliphoridae	
Rhyncomya viridaurea (Wiedemann)	Nectar
Chrysomya megacephala (F.)	Nectar
HYMENOPTERA	
Formicidae	
Camponotus sericeus (F.)	Nectar
Camponotus sp.	Nectar
Solenopsis geminata (F.)	Nectar
Paratrechina sp.	Nectar
Sphecidae	
Chalybion bengalense (Dahlbom)	Nectar
Vespidae	
Ropalidia spatulata (Vecht)	Nectar
Polistes stigma tamula (F.)	Nectar
Vespa sp.	Nectar
Apidae	
Trigona sp.	Nectar
Apis cerana indica (F.)	Nectar & Pollen
A. florea (F.)	Nectar & Pollen
ARANEAE	
Oxyopidae	
Oxyopes birmanicus (Thorell)	Predates mostly on flies
Thomisidae	Predates mostly on flies
Thomisus sp.	
Salticidae	
'Unidentified'	Predates mostly on flies

concentrations measured at 3-hourly intervals from 0600 to 1800 h (Table 3) show a gradual rise up to 1500 h, of course not to appreciably high levels, and thence a gradual fall. The lowest concentration recorded is 25% and the highest 32%.

Sugars in nectar. The sugars and their relative amounts per μl are glucose (0.11 mg), fructose (0.095 mg) and sucrose (0.025 mg). The nectar is glucose plus fructose dominated, with a ratio of glucose + fructose/sucrose of 8:2; it is characteristic of unprotected open nectaries (Percival 1961).

Aminoacids in nectar. They are present and the score on histidine scale is 6.

Proteins in nectar. A faint greenish blue colour with the bromo-phenol blue stain on

Photographs of insects at the cyathial clustures of *Euphorbia geniculata: a - Trigona* bee lapping on the nectar; b - wasp (*Ropalidia spatulata*) lapping on the nectar; c - ant (*Camponotus* sp.) taking the nectar; d - beetle (*Coccinella repanda*) taking the nectar; e - beetle (*Verana discolor*) taking the nectar.

the chromatographic paper with nectar drop dried, indicates the presence of proteins but in meagre amounts.

INSECTS ACTIVITY DYNAMICS

Composition. A list of the insect visitors in the population are available in flower during April-September. Table 5 gives the relative frequency of different foragers classed under the arbitrary groups: ants, wasps, beetles, bees, and others of rare occurrence in different months.

TABLE 5

SEASONAL VARIATION IN THE DIFFERENT GROUPS OF INSECT FORAGES AT *E. geniculata* FLOWERS

Sampling day	Ants	Wasps	Beetles	Bees (*Trigona*)	Total	Simultaneously blooming associated plant species
1979						
17 April	165	56	68	0	289	E, Pe, So.
17 May	142	96	10	0	248	A, B, E, Pe, Ph, So, Sor.
20 June	258	118	17	0	393	Am, B, C, E, J, La, Pe, Ph, So, T, Z.
23 July	225	121	0	0	346	Am, C, E, J, La, Le, Pe, Ph, So, T, Z.
29 August	123	37	0	0	160	Am, C, E, J, La, Le, Pe, Ph, So, T.
9 September	136	68	0	102	306	Am, C, E, La, Le, Ph, So, T.
1980						
7 June	249	127	33	0	409	Am, B, C, J, La, Pe, Ph, So, T.
5 July	232	77	28	0	337	Am, C, E, J, La, Le, Pe, Ph, So, T.
24 August	163	95	11	0	269	Am, C, E, J, La, Le, Ph, Sor, T.
21 September	124	86	14	136	360	C, E, La, Le, Pe, Ph, T.
29 December	95	22	68	0	185	B, C, E, La, Sa, T.

Am — *Ammonia baccifera*; Ar — *Arachis hypogea*; B — *Brassica nigra*; C — *Croton bonplandianum*; E — *Euphorbia hirta*; J — *Jatropha gossypiifolia*; La — *Lantana camara*; Le — *Leptadenia reticulata*; Pe — *Pennisetum typhoideum*; Ph — *Phyllanthus niruri;* Sa — *Sapindus emarginatus;* So — *Solanum nigrum*; Sor — *Sorghum vulgare*; Tr — *Tridax procumbens*; Z — *Zea mays.*

collected during the entire period of the study is furnished in Table 4, and those insects photographed at the cyathia are given in Plate I. Of the 30 species, 7 belong to Coleoptera, 11 to Hymenoptera, 8 to Diptera, 1 to Heteroptera, and 3 to Araneae; the activity of 27 of these is mainly directed to collection of nectar, the other three, not to be recognised as visitors in the sense of pollination ecology, are predators and simply await the arrival of their prey (mostly Dipterans) at the cyathia.

Seasonal periodicity. During 1979 the plants

Both ants and wasps visited the flowers throughout the blooming period, but in every month ants predominated. Beetles appeared from April and persisted only till June; their number in April exceeded those of the wasps, but thenceforth maintained at a lower level. Bees, mostly *Trigona* were only evident in September, and are next to ants in abundance.

In 1980, because of delayed onset of monsoon rains, the plants in flower were available from June onwards. Right then, ants, wasps, and beetles started visiting. As in 1979 ants frequented more. Beetles were less frequent all through the period. In September as usual *Trigona* appeared in relatively large numbers. From October to November the plants were not available because of some weeding practices, but by December some were evident and ants, wasps and beetles were seen visiting them in considerable frequency.

It is surprising that *Apis* species which have been observed on most plant species of the Visakhapatnam flora are very rarely noticed at the flowers of *E. geniculata.* Why these honeybees shun *E. geniculata* flowers? Probably as reported by Deodikar *et al.* (1958), the forage of this plant may be poisonous to these bees; these authors reported an instance of large scale paralysis and deaths among bees due to their foraging on flowers of *E. geniculata.* However, Deodikar (1961) remarks that such plants may be visited due to acute hunger and starvation in times of acute shortage of normal forage during floral gap periods.

Diurnal periodicity. Figure 3 illustrates the activity pattern of different arbitrary groups of insects studied for half an hour at 1-hourly intervals in different months but represented as pooled up data. Though ants forage on nectar during the whole day, the activity pattern is measured only during daytime. Their activity from 0600 h gradually increased to a maximum by 1030 h and decreased slowly to lower levels up to 1330 h but again revived and kept on increasing till the end of observation period. The activity pattern of wasps and beetles is identical with each other. The number of visits rose to maximal levels between 0730-0830 h, and then declined rather gradually to minimal levels by 1330 h, but again the activity slightly resurged and continued till it ceased with the set in of dusk. *Trigona* bees were evident from 0700 h onwards till they disappeared with the set in of dusk. The activity increased rather slowly up to the 0830 h, but then showed a sharp rise to a maximum in the next hour; thence there was a gradual decline to lower levels up to 1200 h when again there was a resurgence increasing to a considerably higher level by 1630 h from then onwards the activity fell abruptly.

There is a clear indication of relationship of insect activity with the temperature. In general the activity kept on increasing in parallel with the temperature but up to certain temperature levels which varied with the different groups. Thus ant activity increased up to 1030-1130 h, when the ambient air tempera-

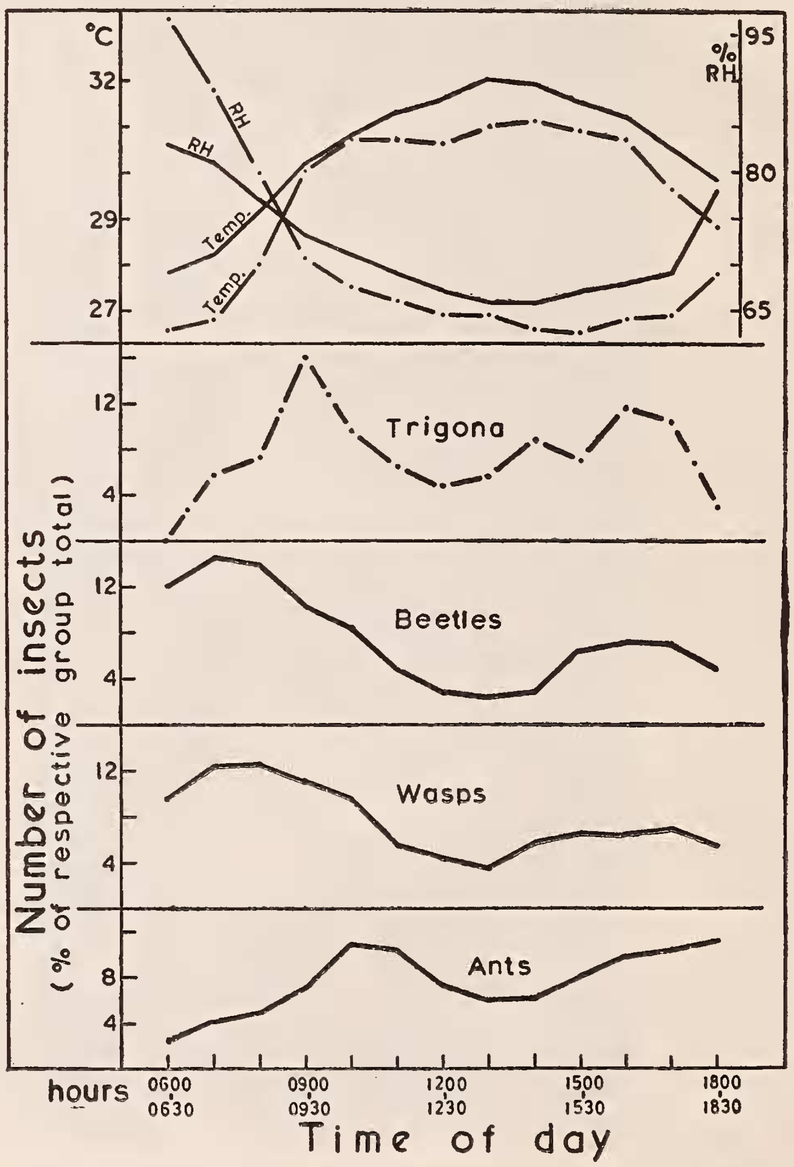

Fig. 3. Diurnal variation in the number of different insects visiting the cyathia of *Euphorbia geniculata* related to the prevailing temperature and relative humidity.

Table 6

Temporal variation in pollen depletion from anthers vs. pollen deposition onto stigmas of *E. geniculata* under insect activity

Time (h)	Mean No. of pollen depletion/ flower	Rate of pollen depletion (%)	Mean No. of pollen deposited onto stigma	Rate of pollen deposition (%)
0800	0	0	0	0
1000	174	47.0	18	41.9
1200	82	22.2	13	30.2
1400	35	9.5	5	11.6
1600	32	8.7	6	14.0
1800	14	3.8	1	2.3
	(n = 10)		(n = 20)	

tures were 30.8-31.3°C, wasp and beetle activity was brisk between 0730-0830 h when the air temperatures were 28.2-29.1°C, and *Trigona* activity increased up to 0930 h when the air temperature was 30.1°C. With further rise in temperature the activity tended to decline till 1330 h. From then onwards, it was revived with the downward trend in temperature. *Trigona* bees appear to dislike to work at high humidities, as they have not appeared before 0700 h when high humidities prevailed.

Pollen depletion v. pollen deposition on to the stigmas under insect activity. Predictably there is an inverse relationship between pollen depletion from the anthers and pollen deposition onto the stigmas (Table 6). Most pollen (69%) is removed by noon and 72% of the total stigmatic pollen loads is getting deposited by then.

Determinations of the pollen content of anthers dropped off the stamens revealed that *c.* 9% of the total pollen output may remain without removal by the insect activity.

Visits per unit time, and the time spent on cyathia per visit. As is obvious the time spent by a visitor on a cyathium is inversely related to the number of cyathia it visited per unit time (Table 7). Wasps are mobile spending *c.* 3 seconds on a cyathium and visiting 15 cyathia in a minute, followed by *Trigona,* ants, and beetles in that order.

Pollen pick up and pollen transfer onto the stigmas. The ability to transfer pollen onto the stigmas is directly related to the ability of a visitor to pick up pollen, both are a function of body size of the respective insects. Wasps being relatively larger in size picked up and moved more pollen than other groups; ants, *Trigona* and beetles follow wasps in that order (Table 7).

Table 7

Dynamics of the insect activity on *E. geniculata* flowers

Insect variety	Mean No. of insect visits/ minute	Mean length of time at a flower in a visit (seconds)	Mean No. of pollen carried on insect bodies	Mean No. of pollen transferred per single visit	Time spent towards foraging/ minute (seconds)
Beetles	3	14	42	3	34
Ants	11	4	108	4	40
Wasps	15	3	231	6	42
Trigona	13	3	57	1	39
	n = 20	n = 50	n = 5	n = 10	

MODES OF REPRODUCTION

Table 8 represents the results of breeding experiments from which it is evident that the plants are compatible for both geitono- and xeno-gamous pollen with nearly 100% success. Apomixis is totally absent.

TABLE 8

FRUIT AND SEED SET, AND FECUNDITY IN DIFFERENT MODES OF REPRODUCTION IN *E. geniculata*

Treatment	No. of cyathia obser-ved	No. of cyathia set fruit	Fruit set (%)	Seed set (%)	Fecun-dity (%)
Apomixis (Emasculated and kept under insect exclo-sures)	475	0	0	0	0
Geitonogamy	77	75	97.4	97.4	97.0
Xenogamy	85	84	98.8	100.0	98.8
Open pollination	568	568	100.0	95.5	95.5
Under insect exclosures	496	65	13.0	47.8	6.7

DISCUSSION

The cyathium, though consists of many male flowers (each in the form of a single stamen) and one terminal female, is ecologically equivalent to a flat simple blossom (Knuth 1906-9). Such a floral device is very economical both to the plant and the animal visitor (Grant 1976). The Cyathia in *Euphorbia geniculata* are markedly protogynous, thus precluding pollination within a cyathium and also establishing a potential for outcrossing and the resultant genetic variability. In a cluster of cyathia, different staged ones are evident, such that on any day some cyathia would be in a female stage and some in a male stage.

Of the different groups of insect foragers at the cyathia (Table 4), ants, wasps, and beetles are treated as the effective pollinators in the light of the principles propounded by Free and Williams (1977). No doubt other insects included in the table also carry out some pollination.

The dehiscent side of the anthers is directed upwards, and when the insects concerned land in the cyathia and walk about, pollen is deposited sternotribically. Pollen pick-up by the insects in unhindered by the floral device involving the change in position of the pistil in the cyathia (Fig. 2). When the pollen laden insects land and move in the female cyathia they contact the stigmas and effect pollination which may be geitono- or xeno-gamous because the plants are adapted for both modes of reproduction. The cyathia have no closely evolved relationship with any of the pollinating insects, and thus function as a promiscuous floral device in attracting insects (Grant 1949), and relies on 'mess and soil' insect behaviour (Faegri & Pijl 1979) to be pollinated. As such, any insect with sufficient body size to permit contact with the anthers or the stigmas is capable of promoting pollination at least within the plant by its movement.

The major groups of insects associated with the cyathia of *E. geniculata* are similar to those encountered in related species of *Euphorbia.* (Knuth 1906-9, Kügler 1970, Proctor & Yeo 1975, Ehrenfeld 1979), but the individual species are not one and the same. As is expected of a tropical environment, the ants numerically predominated, and are the only pollinators when the plants occur in the fields of *Sorghum, Pennisetum* and maize. The importance of ants as pollinators becomes